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How Classical Segregation Can Fit Within Modern Cell Biological Segregation

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Abstract

In the past century two versions of the principle of segregation have been used in biology, and both can claim to have connections to concepts presented by Mendel. The cytological version applies to all types of cell division and, by achieving transmission of full chromosome sets, acts to conserve the genome. Here independent assortment, not segregation, produces new genetic combinations. Some important features of the cytological version of segregation are consistent with Mendel's law of combination, and with some of his other statements. In contrast, the classical version limits segregation to the separation of differing alleles during meiosis, and segregation and independent assortment can both result in new genetic combinations. A survey of articles from the journal Science indicates that recently the cytological version of segregation has increased in use. It is concluded that this cytological/cell biological version of segregation is broader and conceptually more powerful compared to the classical version. This cell biologists' version of segregation should be considered for wider adoption as a useful expansion of the biological principle of segregation.

Keywords: assortment, Bateson, cytology, Mendel, Mendelian principles, Morgan, segregation.

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1. Introduction

In the struggle in the early 1900s to define Mendelian genetics there were arguments between several opposed groups of biologists [1-5]. One group, the classical breeders/geneticists, included such people as Bateson [6], Guyer [7], and Punnett [8]. Another group, the early cytologists, included Sutton [9, 10], Boveri [11], Wilson [12, 13], and Morgan [14-16] amongst others. There were large differences in how these two groups viewed many aspects of genetics, with both sides arguing that their view was the one that was widely accepted [17 pp. 23; 18, pp. 35].

In this article I will describe how many features currently attributed to two very different versions of the principle of segregation can be traced back to these two groups. Also, in comparing these two versions, it will be argued that one can be seen as a subset of the other, with each version focusing at a different level of organization and having many different features. Thus the principle of segregation is suggested to have been expanded beyond its classical limits, and the features and applications of this new expanded version need to be more widely appreciated. But first, to establish the proper context, it is necessary to give a brief outline of the thinking of each of these groups of biologists relative to segregation.

The classical view of segregation was associated early on with the suggestion that there could be a physical absence of certain genetic factors, which was seen as a way to account for Mendelian recessive phenotypes [18-20]. This “presence and absence” hypothesis [21] was also thought to apply during “somatic segregation”, a concept which attempted to account for differentiation through a regular loss of some genetic factors during the development of different somatic cell lines [8, 22-28]. Given this thinking, there was some skepticism expressed about whether all the genetic factors were truly associated with the chromosomes [7] and about whether the chromosomes should be viewed as relatively stable structures [24, 26, 29]. This group considered segregation to be the means to both separate genetic factors and to form new combinations made up of differing numbers of those factors [30, 31, 32], implying a highly variable genome.

In contrast, the cytologists rejected the “presence and absence” hypothesis; rather mutant alleles were argued to represent physically present though genetically silent entities [13, 17, 33]. This was consistent with the view that sets of genes were conserved in most cell types, including the germ line cells, keeping the chromosome sets consistent as well [15, 34]. Changes to chromosome structure and number were noted to occur, but these were seen as exceptions to the more common rule of chromosome and set stability [17]. There was linkage of genes, arranged linearly in the chromosomes [16, 35]. And some [17, 36], while presenting segregation and independent assortment as distinct principles, also pointed out that it was the behavior of the chromosomes that provided the mechanism for Mendelian segregation.

The classical version of segregation was the form that was widely adopted initially [24, 37]. Indeed, except for a few concepts such as independent assortment, these early breeders and geneticists largely got to define most of the terms used in what we now refer to as Mendelian genetics [5]. Through the 1910s and on, the cytologists had to argue with many skeptics [5, 38] merely to get chromosomes widely accepted as the bearers of the genetic material. In addition, cytologists had to explain how constant chromosomes bearing the same genetic combination were consistent with the phenotypic differences found between different cell types in the same organism [13, 39, 40]. Clearly while recognized as a possibility the chromosome theory was not immediately accepted by all [29]. A benefit of having to confront such skepticism was perhaps that it helped to force cytologists to refine their thinking. But in terms of the meaning of the principle of segregation, the classical version of segregation was dominant from the 1900s on, with the cytological version of this concept having to wait until fairly recently to become more widely adopted.

Today there are two very different versions of the principle of segregation in use, both of which are highly useful as concepts in their respective fields of genetics and cell biology. I will argue that many features of the principle of segregation used in much of the recent literature and taught to students are carried over from the classical version of segregation. This version has broad application as a powerful concept in genetics, but I will describe limitations of some of its features, and will point out examples from the more recent literature that illustrate connections to the views of the early breeders/geneticists. Then I will describe features that the early cytologists discovered, note their importance to a cytology-based version of segregation, and point out examples of their use in the more recent cell biology literature. Changes in the pattern of use of these two views of segregation over the last century will be presented. The way in which Mendel’s publication may have influenced the early cytologists and how some features of the cytological version of segregation can be seen to be consistent with some of Mendel’s statements will be described. Finally I will evaluate these two versions of the principle of segregation, and will argue that cell biologists have developed the cytological principle of segregation into a concept of broader application and power relative to the classical version. With the decoupling of assortment from segregation, the classical version of segregation can be seen to fit within the cell biological version of segregation. Thus the time might be right to consider revising and updating the principle of segregation so that it can be unified, have a broader scope, and better serve as a truly fundamental biological principle today.

2. Classical view of segregation

This version of segregation is the traditional one, and is often presented in many texts. It is largely based on a conception of segregation put forward in the first decade of the twentieth century with the rediscovery of Mendel’s work. Not all the features initially attributed to this version of segregation have been retained, but many of its features that are used today can be traced back to the earlier workers’ conception of segregation. This version finds some of its most powerful applications in studies at the allelic level, in which its similarity to assortment gives a set of clear expectations related to specific crosses. Here the focus will be to describe some of the critical features of this classical version of segregation, noting connections to the earlier literature where appropriate.

2.1 Issues resolved by the classical version of segregation

At the time of the rediscovery of Mendel's work the issue of whether or not the genes were stable units or if there was some sort of blending of the genetic factors was seen by many to be resolved by Mendel's findings and by the work of others [6, 41, 42]. Observing the distinct separation of genetic units (i.e. "segregation") and their detection in later generations were taken as evidence of their stability [43], and this allowed a clear means for testing which phenotypic traits might be attributed to the actions of individual genes. This functional use of a demonstration of segregation as a means to identify monogenic traits is still widely used [44].

2.2 One Mendelian principle: segregation and independent assortment are similar

Interestingly, in the early 1900s, segregation was initially the sole major Mendelian principle, with independent assortment only being defined later [17]. One implication of this was that for over a decade the concept of Mendelian segregation had to account both for how the separation of genetic factors and the formation of new genetic combinations might occur [6, 45-48]. Thus certain features became attributed to segregation which some might now attribute to independent assortment. Even after two distinct Mendelian principles were established there was much conceptual overlap in their application, often making them still in effect a single principle. For instance, in multihybrid situations segregation was often presented as the means by which different factors could segregate "independent" of each other (Table 1d). Thus during such a cross each pair of differing alleles would "segregate" from each other, while in a multihybrid cross each pair of alleles would be doing its own "segregating independently" from other pairs [50]. In this view, both segregation and independent assortment can produce new genetic combinations that are different compared to the parent cell (Table 1a, b, d). The main distinction between these two principles would then be the level of organization at which they operate; with segregation more often associated with monohybrid situations, while independent assortment would more often be applied to multihybrid situations. Underlying independent assortment, the segregation of each individual pair of alleles for a given gene was presumably at work (Table 1f). Therefore segregation tended to be the more prominent concept and was the one that came to have many aspects of Mendelian genetics associated with it.

Table 1. Statements relating to the segregation of genetic material from the classical perspective.

	Quotes and sources:
a	"The great discovery of Mendel is this: The hybrid, whatever its own character, produces ripe germ-cells which bear only the pure character of one parent or the other... This perfectly simple principle is known as the law of 'segregation', or the law of the 'purity of the germ-cells'" [51, pp. 398] .
b	"The leading principle discovered by Mendel was that a hybrid whose parents differ in respect to a single factor of development produces two kinds of gametes, respectively like the gametes of the two parents. This is now known as the law of segregation" [52, pp. 760].
c	"This phenomenon, the dissociation of characters from each other in the course of the formation of the germs, we speak of as segregation, and the characters which segregate from each other are described as allelomorphic, i.e. alternative to each other in the constitution of the gametes..." [24, pp. 11] .
d	"Segregation. Unit characters, although they may be intimately associated together in the individual, during the complicated process of maturation that always precedes the formation of a new individual, separate or segregate out as if independent of each other and thus are enabled to unite into new combinations" [49, pp. 145].
e	"...the law of segregation states that the two alleles for a heritable character segregate (separate from each other) during gamete formation and end up in different gametes" [54, pp. 265].
f	"Mendel's Second Law (Independent Assortment): The alleles underlying two or more different traits are transmitted to offspring independently of each other; the transmission of each trait separately follows the first law of segregation" [53, pp. 19].

This conceptual blending of segregation and independent segregation is also found in the various uses of these concepts in more recent publications. For instance, many texts describe independent assortment as the "independent segregation" of each homologous pair of chromosomes relative to other pairs [54-56]. The use of "independent segregation" and "independent assortment" as synonymous terms further illustrates the conceptual fusing of these two principles [57-64]. In most cases the equivalence of these terms is only implied, but in some cases their equivalence is made explicit as in the reference by Allen [65, pp. 415] to how in their usage "... the segregation of the units - is referred to as 'assortment.'" The fusion of these concepts is also evident in some of the ways that "segregation" is used relative to the movements of differing genetic factors. For instance,

genetic linkage between two genes is in some cases referred to as “cosegregation” [66-73], or there may be reference to “concordant segregation” [74, 75], or reference to “segregation analysis” [76] as a means to determine linkage. In some articles a “failure to segregate” is taken as an indication of linkage between two genes [77, 78], just as a failure to independently assort would also indicate linkage. The implication being, according to this version of segregation, that there should be separation of different genetic factors achieved in the normal course of segregation. This seems to echo some earlier worker’s references to crosses which showed definite segregation [79] in that the separation of distinct unit factors would refute any hypothetical blending of genetic factors. Both segregation and independent assortment were viewed to produce genetic changes relative to the parent cell and were seen to share the same essential mechanism. Thus this classical version of segregation had many conceptual similarities to what later became features of independent assortment.

2.3 Genotypic dependence of segregation

Through the separation of differing alleles, the classical version of segregation produces new genetic combinations relative to the parent cell [8, 80], but for this to occur there must be different alleles present in the first place. Thus a completely homozygous diploid cell would be said to be unable to carry out any segregation [24, 81]. In this view, segregation is dependent on the genotypic state, and so segregation would typically only occur for the heterozygous genes of a diploid hybrid cell (Table 1a, b, c). This limits segregation to genetic hybrids [41]. Thus some genes in the heterozygous state may “show” segregation, while others in the same cell might be homozygous and be said to be “non-segregating” genetic factors [82].

Today such a strict genotypic dependence of segregation, with only genes in a heterozygous state doing it, might seem to some biologists to be a rather extreme position, however aspects of this feature are seen in many studies. For instance, this genotypic dependence of segregation is evident in work that examines “second division segregation” in meiosis, which is said to be dependent on there being crossing over early in meiosis so that different alleles are available in the double chromatid chromosomes to be separated in meiosis II [83-87]. This genotypic dependence of segregation in meiosis II is presented in some more recently published works [56, 88, 89] and in lab manuals [90]. Another way that this genotypic dependence of segregation is illustrated is by references to how hybrids, which are heterozygous for a gene of interest, are said to be able to demonstrate segregation [57, 91-94]. The implication being that homozygous genotypes cannot show segregation, while hybrids can. It may be noted that, since this version of segregation is limited to a heterozygous condition, this largely limits segregation to diploid cells undergoing a reductive type of cell division [48], and places the focus of this concept mainly at the allelic level (Table 2).

Table 2. A comparison of features of the concept of segregation of genetic material that have arisen from the classical perspective, compared to that developed by cell biologists.

Feature:	Classical view of segregation:	Cell biological view of segregation:
Type of cell division in which it occurs:	Meiosis I, and with crossing over may be seen in meiosis II.	Any type of cell division, and division of some organelles.
Cell product formed:	Gamete formation.	Any type of daughter cell.
Genotypic constraints:	Genotype dependent: Must be heterozygous.	Genotype independent: No genetic variation is needed.
Ploidy:	Done by diploids.	Is possible with any ploidy.
Level of application:	Alleles of a gene: Allelic.	Full sets of chromosomes: Genomic.
How related to independent assortment?	A simpler version of the process that underlies independent assortment.	A process distinct from independent assortment.
Function:	Production of new genetic combinations distinct from the parent hybrid cell.	To pass on conserved full sets of the genetic material to daughter cells.

2.4 What cells segregation produces

It is unfortunate that many published descriptions of segregation associate it just with meiosis leading to gamete formation, similar to how the early workers described it (Table 1b, c, e). Given that the life cycle of plants, fungi and many other eukaryotes are known to involve sporic meiosis [95], if segregation is meant to occur only during meiosis, then obviously spores should also be identified as typical products. On the other hand, if gamete formation is instead the critical issue, then it should be recognized that many species create their gametes by mitosis. Given the published references to segregation during sporogenesis [96, 97], the former was clearly the intent. Therefore, reference to the "products of meiosis," so as to include spores and not merely gametes, might be more

appropriate so as not to give the false impression that organisms such as plants make their gametes by meiosis?

This distinction is important not just for definitional reasons. In plants, the existence of the intervening gametophyte generation presents an opportunity for selection to operate at this point in the life cycle. It has long been recognized [98] that in order to treat the frequencies of genotypic combinations found in all of a plant's spores as equivalent to that later found in their gametes it must be assumed that there is no significant selection applied on the gametophyte stage. Yet such a selective effect on the gametophyte has been reported to skew the ratios of gametes that are later made [99, 100], and this selection can be expected to alter the ratios of genotypes seen in individuals in the subsequent sporophyte generation. Thus in species that carry out sporic meiosis, with an alternation of generations life cycle, the expectations from Mendelian genetics are more likely to be met in the immediate products of meiosis, in this case the spores. It may, or may not, be the case that the later population of gametes presented for fertilization will have the same frequencies of genotypes as the earlier spores.

2.5 Summary of the classical view of segregation

The classical conception of segregation has several features often associated with its use today. Its focus is mainly at the allelic level, it is dependent on there being differing alleles present (genotypic dependence), and it has a role in the production of new genetic combinations in the daughter cells made through meiosis (Table 2). Many recent articles portray segregation as being associated with the separation of distinct alleles [64, 72, 93, 94, 101-105], and such use is consistent with the classical portrayal of segregation as associated with genetic change.

However, by not recognizing an association between the behavior of the genetic factors and that of the chromosomes [24], the classical version of segregation lacks a clear mechanistic distinction between it and independent assortment. This conceptual overlap is such that, in this classical view of segregation, to say that different alleles of a gene "segregate" is similar to saying that they "assort." And so in a multihybrid situation the different pairs of alleles can be said to "independently assort" or to "independently segregate." This leaves any mechanistic differences between the two principles rather vague. Instead the conceptual overlap between these two principles may lead segregation to be viewed as a mechanism for achieving independent assortment (Table 1f). This makes segregation the more fundamental of these two Mendelian principles; a situation which may in part be a consequence of the initial attribution of many features of Mendelian genetics to just segregation. Thus, while not all of the features attributed to it early on are completely accepted today (Table 2), many aspects of the classical version of segregation are currently seen in the recent literature and are being taught.

3. Cytologists' view of segregation

In the early 1900s cytologists often referred to segregation in a manner consistent with the classical version of segregation. Indeed, Morgan's [17] statement of the principle of segregation is not significantly different from the classical version being used at that time. However, over time cell biologists have built on some earlier cytological ideas, and now attribute many new features to segregation, making their conception of it today very different from classical segregation. Obviously the more recent cell biological version of segregation did not spring from a vacuum, and so an obvious question is which of its features can be connected back to earlier views of these concepts?

So next I will describe some of the features of this newer version of segregation, noting some connections back to earlier cytological thinking. In doing this I will not attempt to outline all of early cytology, but instead will try to focus on specific issues connected to the cell biologists' version of segregation. Those desiring more details of the early history of cytology might wish to see the following, as well as the items cited in them [34, 36, 106-108].

Table 3. Quotes relating to the genetic concept of segregation from early cytological and later cell biological publications.

	Quotes and Sources:
a	"... another fundamentally important fact that was also proved by Mendel's experiments, namely that in the formation of the simplex character-groups all possible recombinations of the original parental unit-characters (within the limits of a single complete group) are effected" [1, pp. 819].
b	"These facts in connection with the fact that an X egg of a female produces a male if fertilized by an X sperm prove that the segregation of the X chromosomes is the segregation of the sex-differentiators" [115, pp. 162].
c	"Mendel did not emphasize the idea that even in pure races each character is also represented, as a rule, by a pair of factors or genes that segregate in the formation of the germ-cells in the same way as do the pair of contrasted genes in the heterozygotes, but at the present time this idea is accepted by all geneticists" [17, pp. 23].
d	"The faithful inheritance of genetic information depends on the orderly segregation of chromosomes in mitosis and meiosis. Mitotic segregation produces genetically identical daughter cells, while meiotic segregation produces cells that contain only one member of each chromosome pair that was present in the parental cell" [129, pp. 289-290].
e	"In anaphase, all sister chromatids separate in concert and segregate oppositely along the anaphase spindle (towards the spindle poles/centrosomes) into the two daughter cells... In metaphase I, homologous chromosomes are associated, and in anaphase I they segregate without sister chromatid separation... In metaphase II and anaphase II, chromosomes are segregated, as... in somatic cells..." [130, pp. 21-22].

3.1 Genome level of focus

One early cytological concept was that sets of genetic material moved as complete groups (Table 3a). This was consistent with the argument that the chromosomes pass through cell divisions in complete sets; one of the pillars of the chromosome theory of inheritance and consistent with the proposed continuity of the germ plasm [1, 12, 15, 17, 109-112]. In a modern context, we might say that this feature puts emphasis on the movement of complete sets of the genome [113, 114], rather

than just on the movement of alleles. Thus in the early 1900s cytological thinking was often at a broader level of organization (genomic versus allelic) compared to many of the early geneticists (Table 2). It took several decades for most cytologists to connect this feature to segregation, though there were some who were considering issues above the level of the alleles early on (Table 3b). So, while in the early 1900s the classical definition of "segregation" with its focus at the allelic level was still the typical way this term was used, the concept of stability of genetic sets had been established.

3.2 Segregation as a distinct process from independent assortment

With the rise in interest in linkage, the production of new genetic combinations became a focus of many cytologists' work [16, 116]. Once the production of these new combinations was found to involve events distinct from the broad passage of chromosome sets to daughter cells, Morgan proposed independent assortment as a second principle in addition to segregation [17, 117]. By conceiving of two Mendelian principles, where before there was only one, Morgan created an opportunity for others to later consider how each principle might use different mechanisms and accomplish different functions.

3.3. Segregation as essential for genomic stability

Extending the issue of the stability of the germ plasm, the cytological version of segregation also suggests that this process has as one of its critical features the production of viable daughter cells; its failure leading to genetically abnormal cells [118-125]. For viability to be achieved it is necessary to pass on the chromosomes in complete sets. In this way the early geneticists' view of development involving the differential transmission of the genes themselves [18], through "somatic segregation," was also rejected, and replaced in the cytological/cell biological version with a vision of greater genomic stability [114].

3.4. A mechanistic view leading to genotypic independence of segregation

With other processes producing new genetic combinations under specific and limited conditions [126], cytologists came to view segregation as a process that not only occurs in hybrids but in the homozygous condition as well (Table 3c), and so segregation came to be viewed as being independent of genotype (Table 2). Here I will outline some of the thinking that led to this shift, and its implications.

As noted previously, one of the key strengths of Mendelian genetics is its ability to make definite predictions under certain conditions. Thus an F1 monohybrid cross, with a strict dominant/recessive relationship of alleles, should give a 3:1 ratio of phenotypes in the F2 generation. In describing the sex linkage of eye color in fruit flies, Morgan [128] noted how a mating of a heterozygous red-eyed female and a red-eyed male gave a 1:1 ratio of red to white eyes in the offspring. He then argued that, even though this cross failed to give the classical 3:1 phenotypic ratio, it did not refute Mendelian genetics, rather Morgan pointed out how sex linkage of this gene demonstrates a confirmation of Mendelian genetics. Thus it was not the ratio of offsprings' phenotypes that mattered, but that fact that "... the chromosomes have followed strictly the course laid down on Mendel's principle for the distribution of factors" [128, pp. 106]. Indeed, Morgan [128; pp. 82-83] noted how the movements of the chromosomes provide a "mechanism" for Mendelian heredity. In order for Morgan to make his argument, Mendelian genetics had to be shown to be able to be expanded to include the

case of sex linkage, and so he shifted the criteria: Instead of just needing to observe a certain type of phenotypic ratio to confirm a Mendelian model, he argued that another way to identify a "Mendelian" situation would be for the mechanism underlying the production of that ratio to be found to operate in its normal manner. Morgan [127], along with others [36], had noted that the mechanism in this case involved the movement of the chromosomes through the stages of meiosis.

Thus the chromosome movements would account for how the differing alleles in a heterozygous situation would end up in different daughter cells. Meiosis I was argued by Morgan [128] to be one type of cell division in which segregation must occur. Other cytologists had made the suggestion that the key focus of segregation should be about how the chromosomes behave (Table 3b). Viewed in this way, the separation of differing alleles can be seen as merely a specific case that arises through the functioning of this mechanism, although it is a useful case as it allows for easy detection of the chromosome behavior via the genetic differences produced. However, since the mechanism operates no matter whether the genes are homozygous or heterozygous, segregation came to be seen as happening not only in the hybrid state (Table 3c), but would also occur in the homozygous state of pure breeding lines as well. Thus the segregation that occurs in meiosis I can be seen as being independent of genotype, and it has as one of its major functions the separation of full sets of the chromosomes to ensure germ plasm stability. While carrying out this process, any genes that happen to be in a heterozygous condition would normally be separated as a side consequence. Thus, by altering the focus of segregation from the alleles to the chromosomes, and on to the full genome, a shift in the main function of segregation was achieved (Table 2).

3.5. Segregation during any type of cell division

This expansion of the concept of segregation was taken still further by later cell biologists. For if segregation normally occurs in meiosis I no matter what the genotypic combination, then it also can be argued that in any normal meiosis II there should always be segregation occurring as well, since here again full sets of chromosomes have to be properly separated to make viable daughter cells. Extend this logic from this early cytological line of reasoning, and the cell biological version of segregation can be seen to be essential in any type of cell division (Table 2). Thus, cell biologists often say that a cell undergoing proper meiosis (Table 3d, e) must have segregation achieved in both meiosis I and in meiosis II [129, 131-133]. The process is also said to be needed for proper passage through mitotic divisions [134-140], and for proper binary fission in prokaryotes [141-146], as well as for the segregation of prokaryotic plasmids [147-149]. The concept has also been applied to the segregation of viral genomes [150]. Aspects of the mechanism by which segregation of the chromosome sets is achieved and how it is regulated during cell division is an area of active research [151]. So, while the classical version would limit segregation just to certain situations in meiosis, the more recent cell biological version extends segregation to any type of cell division including that done by prokaryotic cells.

Table 4. Proposed modern statements of the genetic principles of segregation and independent assortment as derived from the views of the early cytologists and of modern cell biologists.

Principle of Segregation: There is transmission of the genome as a full viable set, or sets. This is normally achieved during anaphase of mitosis, anaphase I and II of meiosis and during binary fission in prokaryotes. At the allelic level, segregation ensures that alleles[1] of a gene are separated; at the chromosome level, it ensures that each chromosome is separated from its equivalent[2]; and, at the genomic level, it ensures that full sets (typically either 1N or 2N sets) of the genome are separated into the resulting daughter cells.
Principle of Independent Assortment: This depends on there being genetic differences present to assort. If so, then new combinations of genetic factors can be produced. Each pair of differing alleles assorts independently from other pairs of differing alleles from which it is genetically unlinked during metaphase I of meiosis, when double chromatid chromosomes line up at the metaphase I plate. And often[3], due to cross over events, there is independent assortment during metaphase II of meiosis between the double chromatid chromosomes which line up at the metaphase II plate, each with different alleles on their chromatids.

[1] The "alleles" need not be different types of alleles for there to be segregation.

[2] A haploid cell in anaphase has genetically equivalent single chromatid chromosomes being segregated. Some argue that, since these two chromosomes are not from distinct parents, it is inaccurate to call these "homologous" chromosomes. Therefore the term "equivalent" is used.

[3] If the allelic pairs are all homozygous or no crossing over occurs, there may be no variation present in meiosis II between the chromatids and, so, no second-division independent assortment.

3.6. Summary of cytological/cell biological version of segregation

Based on its reported features (Tables 2 and 3) and on its uses in the literature, Table 4 gives a cell biology-based statement of the principles of segregation and independent assortment. Notice that here restrictions of genotype, ploidy, and the type of cell division are all shifted to independent assortment, which alone has a role in producing new genetic combinations. Segregation then operates from the genomic level down to the allelic level, and its main function is primarily a conservative one. However, while segregation operates to promote stability of the genome across cell divisions, other processes which can lead to recombinations, via independent assortment or other means, are permitted to take place during meiosis and so can produce new genetic mixtures so long as the requirement of passing on viable genetic sets is achieved. In this way, segregation encompasses the separation of differing alleles during meiosis (one of the main features of the classical version of segregation), and with assortment the classic Mendelian ratios resulting from hybrid crosses can be produced. To produce the classical Mendelian ratios from a dihybrid cross,

there is need for both segregation and independent assortment to occur, while the passage of a fully homozygous cell through meiosis would normally carry out only the process of segregation as there would be no differing pairs of alleles to assort independently. To give one example of the application of the conservative nature of this version of segregation, consider the following: It is evident that proper segregation during mitosis by a plant spore, and by cells of the subsequent gametophyte, must be achieved if the ultimate gamete that will be formed later in the plant life cycle is to have the same combination of chromosomes as found in the initial spore. Thus, this conservative function of segregation often makes the plant spore and gamete genetically equivalent, which explains how it is possible for many workers to treat them as genetically similar items.

This view of segregation goes beyond meiosis and is involved in all types of cell division in a genotypic independent manner. Thus, whether the cell division is meiosis, or mitosis or binary fission, proper segregation is needed to ensure viable daughter cells. This version of segregation has relevance for the production of many types of cells, not just gametes or spores, and so it has numerous important developmental consequences. This version of segregation is also independent of ploidy, in that it needs to be done properly no matter if the cell is diploid or haploid (Table 2). By this view, segregation is a fundamental genetic process that is essential for the proper transmission of the genome needed to ensure viable daughter cell production.

4. Uses of these two versions of segregation over time

These two views of segregation (Table 2) have existed side-by-side in the literature down to today, but when did this newer cell biological version start showing up in publications and how widely used is it today? To explore this, articles in the journal Science that made use of some version of a genetic concept of segregation were examined. Those articles that used the term “segregation” to mean the separation of non-genetic items were excluded, leaving 190 articles, published from 1900 into 2011. The journal Science was chosen as its breadth of coverage included articles from both perspectives, with some articles written by members of the early geneticists and breeders, and others by the early cytologists.

Table 5. A survey of papers from the journal Science that use the indicated features of the principle of segregation, from the year 1900 into 2011.

Features compared:[1]	Percentage of articles using the aspect of each feature compared with in each period. (Number of articles.)					
	1900-1919	1920-1939	1940-1959	1960-1979	1980-1999	2000-2011
Segregation and independent assortment are similar:	93.8 (15)	85.7 (12)	91.7 (11)	76.9 (20)	62.3 (33)	29.4 (20)
Segregation and independent assortment differ:	6.2 (1)	14.3 (2)	8.3 (1)	23.1 (6)	37.7 (20)	70.6 (48)
Focus at allelic level:	93.3 (14)	75.0 (9)	91.7 (11)	68.2 (15)	60.8 (31)	29.9 (20)
Focus at genomic level:	6.7 (1)	25.0 (3)	8.3 (1)	31.8 (7)	39.2 (20)	70.1 (47)
Segregation is genotype dependent:	93.3 (14)	83.3 (10)	91.7 (11)	76.0 (19)	61.5 (32)	27.9 (19)
Segregation is genotype independent:	6.7 (1)	16.7 (2)	8.3 (1)	24.0 (6)	38.5 (20)	72.1 (49)
Segregation in meiosis only:	100.0 (8)	100.0 (12)	85.7 (6)	65.0 (13)	60.0 (24)	25.9 (14)
Segregation in any cell division:	0.0 (0)	0.0 (0)	14.3 (1)	35.0 (7)	40.0 (16)	74.1 (40)
Segregation leads to just gametes:	75.0 (9)	63.6 (7)	66.7 (2)	23.1 (3)	16.7 (3)	7.9 (3)
Segregation leads to various cells:	25.0 (3)	36.4 (4)	33.3 (1)	76.9 (10)	83.3 (15)	92.1 (35)

[1] Details of individual articles are given in the appendix.

In these articles references to “segregation” were evaluated in terms of five differences between the classical and cell biological versions (Table 5): 1) Whether the principles of segregation and independent assortment were used in a similar or in a distinctive manner. For example, instances where segregation was presented as producing genetic change compared to the parent cell, or

where failure to properly segregate implied a lack of independent assortment, were taken as features similar to those of independent assortment. In contrast, when proper segregation was used to imply genetic stability or as normally happening in a haploid cell undergoing mitosis, this was taken as being distinctive from independent assortment. 2) Whether the focus was at the allelic level or was more at the genomic level. For example, references to whole chromosome movements that did not identify specific allelic states were taken to be at the genome level. Descriptions focusing on the separation of alleles from an initial monohybrid condition were considered to be at the allelic level. 3) Was segregation said to depend on the presence of differing factors (i.e. genotype dependent), or did segregation occur no matter what genotypic combinations were present (i.e. genotype independent)? For example, if for a haploid cell undergoing normal mitosis there was mention of segregation of the chromosomes, this was treated as a case of genotype independent segregation as different alleles were not likely to be present if proper replication had been done. 4) Was segregation said to only occur in meiosis, or was segregation said to occur as well in other types of cell division? Papers that applied segregation to mitosis or binary fission were put in the later category. 5) Did segregation result in just gamete formation, or did segregation take part in the production of many different cell types such as somatic cells? Those articles in which the use of an aspect of one of above features could not be designated, or for which use was made of both aspects of a feature, were excluded from the summation given in Table 5. Thus. even though a given time interval had the same set of articles examined, their different uses of the above features often altered the number of articles indicated for a given feature. For each pair of aspects of a feature being compared in Table 5, the upper row reflects the classical view, and the lower row reflects the cell biological view.

It is apparent (Table 5) that well past the 1950s most of the articles followed the classical view of segregation. Thus this version is the more historic one, which is consistent with its being the version that is widely taught. However from the 1960s onward more articles started to use aspects of the cell biological version of segregation. It might be inferred that, with recognition of DNA as the genetic material and with the availability of better techniques for study of the chromosomes, more papers using segregation from the cytological perspective began to be published from the 1960s on. Since cytologists (Table 3b) had already presented the idea that the behavior of the chromosomes was the basis for classical segregation, this shift of focus in these studies to full sets of chromosomes was a natural extension. For this group of articles from Science, 48 out of 68 articles used the cytological/cell biological version of the principle of segregation during the time from the year 2000 into 2011. This suggests that this version of segregation has been adopted recently by a wide number of researchers.

The presence of aspects of both of these views of segregation in recent publications (Table 5) confirms that these two conceptions of segregation are not mere historical oddities, but are actively in use today. Just as Morgan [17] and Punnett [18] put forward very different views of genetics, in more recent times contrasting views of the principle of segregation are found. For instance, when a major cell biology review [129] described the broad general features of segregation as seen in mitosis and meiosis, in that same year scholars of Mendel [81] portrayed segregation in the classic manner by noting that it would only occur when there are genetic differences present to be separated; precluding its normal involvement in mitosis! While many general textbooks present segregation in a manner that is largely consistent with the classical conception of it [54, 56, 152], cell biologists have been attributing new aspects to segregation that, in total, portray a very different view of this biological principle [78, 114, 140, 144, 147, 153-155].

5. What Mendel stated: law of combination

Next we come to the interesting issue of how after its rediscovery the breeders/geneticists viewed Mendel's work in a different manner compared to the cytologists/cell biologists: Could one group of biologists read Mendel's work and conclude that its main focus was about genetic change, while other biologists might read Mendel's work and found in it suggestions of a need for genetic stability? Allen [156] points out that over time different connections have been made to Mendel's work, and suggests that one reason for this is that Mendel was not very explicit in terms of which of the concepts he presented were meant to be closely associated with a given genetic principle. Indeed, as pointed out by Monaghan and Corcos [117], Mendel did not use the exact phrase "law of segregation" or "principle of segregation" in his publication. Without a clear indication of what features should be the core of Mendelian genetics, it was natural that after Mendel's work was rediscovered there were debates. For instance, some [32, 51, 157] suggested a "law of dominance" as the main Mendelian principle. However Bateson [6, 24] instead argued for a focus on segregation as the main result of Mendel's work, based as it was on the existence of non-blending unit factors, leaving dominance as a less central concept. Thus, while the concepts embedded in what came to be called "Mendelian segregation" were indeed presented by Mendel, it was left to others to argue over which actual features presented by Mendel would best fit into what ultimately became the classical principle of segregation. Influencing this debate was the fact that the concept of "segregation" of genetic factors had been raised by others well before the rediscovery of Mendel's work [158, 159], thus this argument over what constituted "Mendelian segregation" was done in a certain context. At the time of the rediscovery of Mendel's work, a major concern of these early workers centered on resolving the issue of whether or not genetic factors were distinct units, and so could be shown to be able to be separated, or if there was blended inheritance [160, 161]. How the connections that many of these early workers found to Mendel's writings led to the development of the classical version of segregation has been well described by others [6, 18, 24, 81, 117, 162-169] and is widely presented in many general texts.

In contrast, I have not found any recent publication which describes how a cytological reading of Mendel's work might reveal connections to concepts that are critical for a later cytological version of segregation. So I will here continue in the long tradition that Allen [156] notes and suggest some new connections that might be made to Mendel's published work. In doing this, I will examine statements from Mendel's publication (Table 6). I should note that I do not mean to imply that Mendel himself anticipated modern genetic concepts such as the genome, rather my intent is to attempt to point out how cytologists who read Mendel's work could find in it ideas that would open a conceptual space for cell biologists who later on crafted their version of segregation. My goal then is to consider how early cytologists might have viewed Mendel's work. Therefore, I have focused on the English translation of Mendel's work that was made available by Bateson [6] because, while recognizing that it is not the only or the most modern translation of Mendel's work available to us today, it certainly was widely read by cytologists in the early 1900s.

Table 6. Statements by Mendel that early cytologists might read as being consistent with the chromosomal theory, and related to the later cell biological version of segregation. Using the English translation as given by Bateson [6].

a	"... the offspring of the hybrids in which several essentially different characters are combined represent the terms of a series of combinations, in which the developmental series for each pair of differentiating characters are associated" (pg 64).
b	"Thereby is simultaneously given the practical proof that the constant characters which appear in the several varieties of a group of plants may be obtained in all the associations which are possible according to the [mathematical] laws of combination, by means of repeated artificial fertilisation" (pg. 65).
c	"The uniformity of behavior shown by the whole of the characters submitted to experiment permits, and fully justifies, the acceptance of the principle that a similar relation exists in the other characters which appear less sharply defined in plants, and therefore could not be included in the separate experiments" (pg. 66).
d	"The hybrids form eight various kinds of egg and pollen cells - ABC, ABc, AbC, Abc, aBC, aBc, abC, abc ... The law of combination of different characters which governs the development of the hybrids finds therefore its foundation and explanation in the principle enunciated, that the hybrids produce egg cells and pollen cells which in equal numbers represent all constant forms which result from the combinations of the characters brought together in fertilisation" (pg. 76).
e	"In *Pisum* it is placed beyond doubt that for the formation of the new embryo a perfect union of elements of both fertilising cells must take place. How could we otherwise explain that among the offspring of the hybrids both original types reappear in equal numbers and with all their peculiarities?" (pgs. 87-88)
f	"This development follows a constant law, which is founded on the material composition and arrangement of the elements which meet in the cell in a vivifying union..." (pg. 88).
g	"... that the behavior of each pair of differentiating characters in hybrid union is independent of the other differences between the two original plants, and further, that the hybrid produces just so many kinds of egg and pollen cells as there are possible constant combination forms" (pg. 89).
h	"The hybrid forms as many kinds of egg cells as there are constant combinations possible of characters conjoined therein..." (pg. 91).

While he made no explicit reference to a “law of segregation”, there is a law that Mendel actually mentioned, which he called a “law of combination". It states that starting with a multihybrid the genetic factors should be divided up only to form certain “combinations” (Table 6a, d). One feature of the “possible” combinations made is that “each pair” of factors must have a representative present (Table 6a, h). Here some could take Mendel to be implying that there was a limit on what sorts of combinations should be considered. For instance, Mendel notes that what might be formed from a trihybrid (AaBbCc) includes combinations such as “aBC” and “AbC” (Table 6d). However a zygote similar to that which might be formed from the fusion of these two combinations could, in principle, also be formed if a gamete containing the combination “AaBb” fused with another gamete which contained “CC.” But Mendel did not list those as possible combinations, and so Mendel’s law of combination implicitly excludes such partial sets. This implies that these factors must move through the gametes as full sets so that only one version of each gene is typically carried by a gamete, which leads to the idea of genetic “purity of the germ-cells” (Table 1a). These limits on the possible combinations along with the independence between factors were noted by Mendel as his major findings (Table 6g). In considering a new plant embryo, Mendel noted how its formation required “a perfect union of elements of both fertilizing cells” (Table 6e). Since such perfection is unlikely to be achieved if gametes contained unequal sets of elements, the implication is that the sets must be genetically complete, though the allelic versions might vary between any two sets. For cytologists it may well have been only a small leap from this focus on the pairs of factors Mendel described to consideration of homologous pairs of chromosomes (Table 3b), and on to the conclusion that the “combinations” Mendel mentions must each occur in a “complete group” (Table 3a), which to some cytologists implied a full set of chromosomes [1, 13]. Thus the transmission of complete sets of genetic material was seen by some cytologists to be the critical feature needed for achieving what Mendel calls a “vivifying union” of factors in the embryo (Table 6f). This thought was echoed by Morgan [170], who noted that orderly and consistent segregation must occur to ensure viability.

Another critical issue for cytologists that can be argued to have connections to Mendel’s publication relates to his statement that those factors which he could not easily study might be assumed to behave in a manner similar to those he could study (Table 6c). Morgan [17], following on an earlier suggestion by Wilson [12], noted that this meant the Mendelian principle of segregation applies “not only to hybrids” (Table 3c). Thus, whether easily detected or not, and regulated in what was then an unknown manner, cytologists recognized that the factors moved as full sets of genetic material [109] and that this movement must occur no matter whether any individual gene happened to be homozygous or heterozygous.

Therefore, when early cytologists read Mendel’s work (Table 6), they were likely to have seen connections between some of his statements, including those relating to his law of combination and their chromosome theory [12, 115, 171]. This opened up the needed conceptual space for other cytologists/cell biologists much later to view segregation as a regular process [119] involving the conservation of sets of chromosomes [40], which logically led in the more modern view of its having a role in the stable transmission of the genome. Thus, key features of the cytologically-derived version of segregation can be argued to have logical connections back to aspects of Mendel’s work. These issues were largely not noticed by the early geneticists and breeders because, as pointed out by Monaghan and Corcos [165], their focus on the separation of genetic differences led them to make other connections to Mendel’s work, and so for them the Mendelian law of combination seemed unimportant. It is apparent that both groups of biologists could find connections to Mendel’s work for many of the features of each of their views of segregation, and therefore it may be argued that both versions have valid claims to being called “Mendelian.”

6. Conclusions

The cell biological version of segregation (Table 4) differs in significant ways from the classical version that was devised by earlier workers. However, often only the classical version of segregation is presented in many genetics [44, 53, 56] and introductory biology texts [54, 152, 172], and, when the behavior of the chromosomes through mitotic cell division is considered, the term “segregation” is often not applied. This raises the issue of how these two versions relate to each other, and when the term “segregation” should be applied. After a brief consideration of these two versions relative to each other, I will argue that many features of the classical version can be fitted within the cell biologists’ version of segregation, making the later the broader form of what can be argued to be one biological principle.

Clearly the classical version of segregation has some unfortunate attributes: including its focus on just the production of gametes as the only type of cell produced, and its conceptual overlap with the principle of independent assortment making what should be two distinct biological principles very similar. Also, given its limitation to meiosis, to a diploid cell, and often to just certain genotypic conditions (Table 2), the classical version excludes many aspects of the cell biologists’ version. Thus, when considering segregation from this classical perspective, we must recognize that, compared to the cell biological version, it is a narrower and more limited version of segregation. In fairness, there are strengths found in this version as well: one is its historic nature, as it is the earlier version of segregation and so has been widely used; another is that it can be a powerful concept when focusing at the allelic level for obtaining a clear estimate of the expected ratios of phenotypic classes for well defined crosses, although whether these outcomes are due to the actions of “segregation” or of “assortment” is often not made clear.

On the other hand, the cell biologists’ version of segregation can be argued to be consistent with many of Mendel’s own statements. Also this version of the principle of segregation has a very distinctive function relative to independent assortment (Table 2). One other important difference that the cell biologists’ version of segregation has compared to the classical version is that in every normal meiosis there should always be proper segregation occurring in meiosis I and meiosis II. The separation of differing alleles for a gene does not indicate segregation to any greater extent than does the separation of similar alleles for a gene (Table 3c). The separation of differing alleles is more often examined merely, as Morgan [17] noted, because the assortment of differing alleles is more easily detected than that of similar alleles; but the similar ones also get separated. Segregation is thus a conservative and consistently necessary process, operating more broadly and in a manner more distinct from independent assortment than is suggested by the classical version of segregation. Thus how the differing alleles for different genes end up in different combinations can be said to be related to how they each “assort”, and so in multihybrid situations that “assortment” would be said to be done independently between genetically unlinked sets of genes (Table 4). Coupling the assortment of differing alleles to the concept of independent assortment and leaving segregation as a conservative process removes the conceptual overlap of these two principles that is seen in the classical version, making the cell biologists’ version clearer relative to the classical version. With segregation occurring through a distinct set of mechanisms relative to independent assortment, it can make use of a distinct set of regulatory systems and be dependent on the activity of different gene products [139], showing again how this version of segregation is distinctive from independent assortment. Applying as it does to many types of cell division, ploidies, and genotypes (Table 2), the cell biologist’s version of segregation is thus broader than the classical version. Indeed, it is broad enough to include in its scope key examples that are often used to portray the classical view of segregation. Thus a monohybrid cell that is separating two differing alleles during meiosis can be seen as a special, though narrow, case which falls within the cell biologists’ version of segregation.

Also, with segregation occurring in prokaryotes, well before the evolution of independent assortment in eukaryotes, this version of the principle of segregation is positioned as being the more ancestral process compared to independent assortment. Thus the cell biologists' version of segregation is broader, clearer, and conceptually more powerful than the classical version. Therefore I would argue that the classical version of segregation can, if properly qualified and distinguished from assortment, be seen as a subset of the broader cell biologist's version of segregation.

Having presented this argument, permit me to anticipate some likely objections. First, it might be argued by some [166] that whether there is segregation in a homozygous case or only in heterozygous situations is a mere matter of semantics. If the focus of interest is at the level of the alleles, as is typical when using the classical version of segregation, then such a view would seem justified, as the separation of similar alleles does not produce different genetic combinations in the resulting cells and a process that produces no differences may seem to be of little interest. However, if the focus is at the genomic level (as is the case with the cell biologist's version), then having proper segregation of the sets of the genome is not a matter of semantics but is the major function that segregation must achieve for viable cells to be produced. Failure of the homozygous genes to properly segregate would imply that events such as non-disjunction may have occurred. So, if viewed from a cell biological perspective, the process matters greatly, no matter whether we can detect it easily genetically or not.

Hartl and Orel [166] also suggest that when cell biologists refer to the separation of chromosomes as "segregation" they are likely confusing it with Mendelian segregation of differing alleles. They note that Mendelian segregation applies only to heterozygous states because that is how it is defined, and suggest that the separation of chromosomes might rather be called "disjunction" to distinguish it from what is done during the Mendelian segregation of differing alleles. But would not such an argument separate the Mendelian segregation concept from its known mechanism? While early in the past century there were those who advocated for such a distinction, mainly because they questioned if all the important genetic factors were truly associated with the chromosomes [24, 29], why we need to impose such a distinction today is not clear. This argument by Hartl and Orel [166] would also seem to reject both the explicit reference (Table 3c) by Morgan [17] suggesting that the Mendelian concept of segregation can be applied to homozygous situations, and also seems to reject the suggestion by Mendel (Table 6c) that his findings might have broad application. Since some of the cytologists' statements [115, 128] imply that the chromosomes give us the mechanism by which Mendelian segregation occurs, it is then only natural that studies of this mechanism should inform us about Mendelian segregation, and some more recent cell biological studies have taken this view (Table 3d,e). Thus associating the Mendelian principle of segregation with chromosomal behavior is justified historically, and is needed if we are to attempt to understand the underlying mechanism of this process. Therefore this is not, as some might suggest [166], a confusion of separate issues, but rather it is an attempt to fully identify the broader aspects of an important genetic concept. What does seem to be evident is that what Morgan stated about these issues (Table 3c) perhaps never was, and may still not be today, "accepted by all geneticists".

Even if, as Hartl and Orel [166] imply, "Mendelian segregation" is seen as a historical concept, and so its definition may properly be fixed as being merely what was stated at a given time in the past, it should still be possible for the concept of segregation to expand beyond the original Mendelian version. Indeed, Allen [156] notes that changes in how Mendelism is viewed have often occurred over time. In that case, while it is appropriate to teach and use a classical definition of "Mendelian segregation," I believe it would be a mistake to limit the modern appreciation of the principle of segregation merely to this historical definition and not recognize how cell biologists have expanded the breadth of this concept. Just as the teaching of evolutionary theory today might find great value in a consideration of a strictly historical view of Darwinian evolution as originally presented by Darwin, few would find it appropriate today to limit one's thinking only to Darwin's original views. Similarly, just because Mendel knew nothing of the mechanisms underlying segregation does not

justify excluding the consequences of the chromosome theory and of other modern thinking when considering a modern biological principle of segregation.

Therefore, if we are not overly dogmatic, biological principles should be revised when warranted, indeed such revising is much of the work of science. I am sure that none would argue that the fields of cytogenetics and cell biology have stood still in the last century, and this activity has produced a version of segregation that seems to offer us a truly fundamental biological principle which is being actively used today, deserving at least some consideration for wider adoption as an important biological concept. Cell biologists should consider more forcefully taking up their valid claims to this broad concept of segregation, acknowledging how it can incorporate many features of the classical Mendelian principle of segregation, and perhaps advocate that other biologists adopt this broader view of segregation for use in publications and in teaching. The result, hopefully, will be a more solid conceptual framework on which to anchor future work, and a grander biological principle of segregation being taught to our students.

In closing, one more quote from Bateson:

“In many well regulated occupations there are persons known as ‘knockers-up,’ whose thankless task it is to rouse others from their slumber, and tell them work-time is come round again. That part I am venturing to play this morning, and if I have knocked a trifle loud, it is because there is need.”

- William Bateson [6, pp. xii] -

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Appendix

A survey of Science articles for uses of the two versions of segregation over time

The details of the designations for five features that differ between the breeders' and the cytologists' versions of segregation, article-by-article, are given below (Table A1). Given that the same set of articles was used, the designation of the features for a given article are not truly independent of each other. For instance, segregation during mitosis is consistent with a conceptual view derived from the cytologists, and therefore other features of their view are likely to also be displayed in such an article. Thus these five features do not represent independent data sets, but rather should be taken as a cross check of each other in terms of the use of the two versions of segregation over time. The two citations noted for Morgan from 1932 [a28] are two installments of one publication, and so were treated as a single article.

Obviously in assembling such a survey of articles there is the possibility of bias introduced due to a variety of factors. One concern is that a given journal might include more articles from one perspective versus the other. For this reason I choose to survey articles from the journal Science as it is broad in coverage and so attracts articles from a variety of perspectives. It also has the advantage of having published articles by prominent members of the two camps, including Bateson and Morgan. It would be interesting to do a similar survey of a journal that specializes in cell biology and of another one that has genetics as its focus, to see if any shift in a similar direction or degree is indicated in their articles for uses of these features of segregation over this same period.

Table A1. Designation of feature usage article-by-article from 1900-2011 for five common features of the concept of segregation. Articles are from the journal Science, and full citations are given in the references for the appendix.

	1) Segregation and independent assortment are		2) Focus is at the level of the		3) Segregation is genotype		4) Segregation is associated with		5) Segregation creates	
Article	Similar	Different	Allele	Genome	Dependent	Independent	Meiosis	Any cell division	Gametes	Diverse cell types
a1 Drew, 1903	x		x		x		x		x	
a2 Bailey, 1903	x		x		x				x	
a3 Castle, 1903	x		x		x				x	
a4 Davenport, 1904	x		x		x				x	
a5 Morgan,1905	x		x		x		x		x	
a6 Guyer, 1907	x		x				x			x
a7 Bateson, 1907	x				x		x			x
a8 Morgan, 1911a	x		x		x		x		x	
a9 Pearl, 1911	x		x		x					
a10 Morgan, 1911b	x		x		x		x		x	
a11 Harper, 1912		x		x		x	x	x		x
a12 Spillman, 1912	x		x		x		x		x	
a13 Smith, 1912	x		x		x					

a14 Webber, 1912	x		x		x		x			
a15 Laughlin, 1913	x		x		x				x	
a16 Bateson, 1914	x		x		x		x	x	x	x
a17 Blakeslee et al., 1920	x			x	x		x		x	
a18 Shull, 1921	x		x				x		x	
a19 Davis, 1922	x				x		x		x	
a20 Mavor et al., 1923	x		x		x		x		x	
a21 Shull, 1924	x		x		x		x		x	
a22 Morgan, 1927		x		x			x			
a23 Stadler, 1928	x		x		x					
a24 Curtis, 1928	x					x	x			x
a25 Dodge, 1929	x		x		x		x			x
a26 Stockard,1929	x			x	x		x		x	
a27 Bressman, 1932	x		x		x					
a28 Morgan, 1932*a* and *b*		x	x			x	x		x	
a29 Dodge, 1936	x		x		x		x			x
a30 Dodge, 1939	x		x		x		x			x

a31 Yarnell, 1942	x		x		x		x			
a32 Garber, 1945	x		x		x					x
a33 Larson and Peng-fi, 1949	x		x		x					
a34 Leng et al., 1950	x		x		x		x			
a35 Pomper and McKee, 1953	x		x		x		x			
a36 Lederberg et al., 1953	x		x		x			x		
a37 Zirkle, 1955	x		x		x					
a38 Lindegren et al., 1957	x		x		x					
a39 Morton, 1958	x		x		x		x		x	
a40 Horsfall and Smithies, 1958	x		x		x		x			
a41 Twitty, 1959	x		x		x					
a42 Newcomer, 1959		x		x		x	x		x	
a43 Sager, 1960	x		x	x	x		x			x
a44 Gerstel, 1961	x			x	x		x		x	
a45 Fatt et al.,1963	x		x		x					
a46 Person and Osborn, 1964		x		x		x		x		

a47 Littlefield, 1964	x		x	x				x		x
a48 Hutton et al., 1964	x		x		x		x			
a49 McFarland et al., 1965	x		x		x					
a50 Jacob,1966		x		x		x		x		x
a51 Lark et al., 1966		x		x		x	x	x		x
a52 Heddle et al., 1967		x		x		x		x		
a53 Gillham and Fifer, 1968	x		x		x			x		x
a54 Leonard et al., 1969	x		x		x		x			x
a55 Jones et al., 1970	x		x		x		x			x
a56 Munck et al.,1970	x		x		x		x			
a57 Bach, 1970	x		x		x		x		x	
a58 Volpe and Earley, 1970		x		x		x		x		x
a59 Ruddle et al., 1972	x		x		x					
a60 Foster et al., 1972	x				x		x			
a61 McMorris et al., 1973	x		x		x					
a62 Lin et al., 1974		x		x		x		x		

a63 Kovithavongs et al., 1974	x				x		x			
a64 Deisseroth et al., 1976	x		x		x					x
a65 Meo et al., 1977	x		x		x		x			
a66 Hickok, 1978	x		x		x		x			x
a67 Moav et al., 1978	x		x		x		x			
a68 Kozak and Rowe, 1979	x		x		x		x		x	
a69 Lin et al., 1980	x		x	x		x		x		
a70 Kovach, 1980	x		x		x		x			
a71 Beamer et al., 1981	x		x		x					
a72 Womack et al.,1981	x		x		x		x			
a73 Stanbridge et al., 1982	x			x				x		x
a74 Sutherland et al., 1982	x		x		x		x			
a75 Shortle et al., 1982	x		x		x		x			
a76 O'Brien and Nash, 1982	x		x		x					
a77 Birky, 1983	x		x		x			x		x
a78 Erlich et al., 1983	x		x		x		x			

a79 Sakaguchi et al., 983	x		x		x					
a80 Evans and Sharp, 1983	x		x		x					
a81 Dawson et al.,1986		x		x		x	x	x		x
a82 Heidmann et al., 1986		x	x		x		x			
a83 Goodfellow et al., 1986	x		x		x		x			
a84 Nathans et al., 1986	x		x		x					
a85 Lemmon et al., 1987	x		x		x		x			
a86 Holliday, 1987	x		x		x		x			
a87 Koshland et al., 1987		x		x		x		x		x
a88 Last et al., 1988	x		x		x		x			
a89 Feldmann et al.,1989	x		x		x		x			
a90 McIntosh et al., 1989		x		x		x		x		x
a91 Xiang et al., 1990	x		x		x		x		x	
a92 Kaback et al., 1992		x		x		x	x			x
a93 Hayashi et al., 1992	x		x		x			x		

a94 Schellenberg et al., 1992	x		x		x					
a95 Gimeno and Fink, 1992	x		x		x		x			x
a96 Bergoffen et al., 1993	x		x		x		x			
a97 Hartwell et al., 1994		x		x		x		x		x
a98 Kroll et all.,1994		x		x		x		x		x
a99 Andersson et al., 1994	x		x		x				x	
a100 Postlethwait et al., 1994	x		x	x	x					
a101 Lander et al., 1994	x		x		x		x			
a102 Vitaterna et al., 1994	x		x		x					
a103 Lai et al., 1994	x		x		x					
a104 Preuss et al., 1994	x		x		x		x			
a105 Levy-Lahad et al., 1995*a*	x		x		x		x			
a106 Levy-Lahad et al., 1995*b*	x		x		x		x			
a107 King et al., 1996		x		x		x		x		
a108 Karpen et al., 1996		x		x		x	x			

a109 Nasmyth, 1996		x		x		x		x		x
a110 Marx, 1996		x		x		x	x			
a111 Elledge, 1996		x		x		x		x		
a112 Stillman, 1996		x		x		x		x		x
a113 Ersfeld and Gull, 1997		x		x		x		x		x
a114 Kirk et al., 1997		x		x		x		x		
a115 Hawley, 1997		x		x		x	x	x		x
a116 Polymeropoulos et al., 1997	x		x		x					
a117 Conrad et al., 1997		x		x		x	x			x
a118 Straight et al., 1997		x		x		x		x		x
a119 Winzeler et al., 1998	x		x		x		x			
a120 Nakamura et al., 1998		x		x		x		x		
a121 Haber, 1998		x		x		x	x		x	
a122 Nurse, 2000		x		x		x		x		x
a123 Mlot, 2000				x		x	x			x
a124 Wang et al., 2000		x		x		x		x		x

a125 Shonn et al., 2000		x		x		x	x	x		
a126 Sluder and McCollum, 2000		x		x		x	x	x		x
a127 Rice et al., 2001	x		x		x		x			
a128 Wu et al., 2001		x		x		x		x		x
a129 Derry et al., 2001		x		x		x		x		x
a130 Katsanis et al., 2001	x		x		x		x			
a131 Schueler et al., 2001		x		x		x	x	x		
a132 Prasanth et al., 2002		x		x		x		x		
a133 Tram and Sullivan, 2002		x		x		x		x		x
a134 Nasmyth, 2002		x		x		x	x	x		x
a135 Percec et al., 2002	x		x		x					
a136 Howlett et al., 2002	x		x		x					
a137 Hall et al., 2002	x		x		x		x	x		
a138 Page and Hawley, 2003		x		x		x	x			
a139 Lee et al., 2003		x		x		x	x	x		
a140 Sherratt, 2003		x		x		x		x		

a141 Selker, 2003		x		x		x		x		
a142 Kitajima et al., 2003		x		x		x	x	x		
a143 Garner et al., 2004		x		x		x		x		x
a144 Møller-Jensen et al., 2004		x		x		x		x		x
a145 Marston et al., 2004		x		x		x	x			
a146 Daniels et al., 2004		x		x		x		x		x
a147 Azzalin et al., 2004		x		x		x		x		
a148 Dynek and Smith, 2004		x		x		x		x		x
a149 Spiliotis et al., 2005		x		x		x		x		x
a150 Indjeian et al., 2005		x		x		x		x		x
a151 Klar et al., 2006		x		x		x		x		x
a152 Hoyt, 2006		x		x		x		x		x
a153 Palframan et al., 2006		x		x		x		x		
a154 Heald, 2006		x		x		x		x		
a155 Armakolas and Klar, 2006	x		x		x			x		x
a156 Haber, 2006	x		x		x			x		x

a157 Barbera et al., 2006		x		x		x		x		
a158 Kim et al., 2007		x	x	x		x	x			x
a159 Mani et al,. 2007	x		x		x					
a160 Travis, 2007		x		x		x		x		x
a161 Lartigue et al., 2007		x		x		x		x		x
a162 Armakolas and Klar, 2007	x				x			x		x
a163 Sapienza, 2007	x		x		x			x		x
a164 Garner et al., 2007		x		x		x		x		x
a165 Folco et al., 2008		x		x		x		x		x
a166 Valle et al., 2008	x		x		x		x			
a167 Morrow et al., 2008	x		x		x					
a168 Seidel et al., 2008	x		x		x		x		x	
a169 Ishii et al., 2008		x		x		x		x		x
a170 Garner, 2008		x		x		x		x		x
a171 Fishman and Saunder, 2008	x		x		x		x			
a172 Rauch et al., 2008		x	x			x	x		x	

a173 Chamberlain et al., 2009	x		x		x					
a174 Akopyants et al., 2009	x		x		x			x		
a175 Salje et al., 2009		x		x		x		x		x
a176 Anderson et al., 2009	x		x		x					
a177 Jensen, 2009		x		x		x		x		x
a178 Musacchio, 2010		x		x		x		x		x
a179 Cheung et al., 2010		x		x		x	x			
a180 Baudat et al., 2010	x		x				x			
a181 Javerzat, 2010		x		x		x		x		x
a182 Youds et al., 2010		x		x		x	x			
a183 Graham et al., 2010	x		x		x					
a184 Mendiburo et al., 2011		x		x		x		x		x
a185 Janssen et al., 2011		x		x		x		x		x
a186 Rambold and Lippincott-Schwartz, 2011		x		x		x		x		x
a187 Keck et al., 2011		x		x		x		x		

a188 Neurohr et al., 2011		x		x		x		x		x
a189 Riehle et al., 2011	x		x		x					
a190 Rosu et al., 2011		x		x		x	x		x	

“I have never written on any subject unless I believed that the authorities on it were hopelessly wrong. If I thought them sound, why write?”

- Samuel Butler (as quoted by Cock et al. [a191, pp. 535]) -

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